

Speciation of the genus *Emmericia* (Gastropoda)

in the Adriatic area

by

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The genus *Emmericia*, proposed by BRUSINA (1870), has attracted much attention from malacologists. Whereas some authors, as for example BRUSINA in one of his papers (1870), considered that only one species existed in the whole area of the genus, others, on the contrary, for example BOURGUIGNAT (1880), drastically went to the other extreme, raising the number of species of this genus even to 67, the ranges of nearly all of which extended to the entire area of the genus. For instance, according to BOURGUIGNAT, in the small river of Jadar, near Split, lived about twenty species of *Emmericia*, whereof the greater number was represented also in the other localities of the Adriatic area. It was a systematics which described the groups of variants of the same species as separate species, without observing the wide intrapopulation variability. No wonder, therefore, that in literature within the genus *Emmericia* there is now a host of names whose synonymy, since the names were given to the various groups of variants in various localities, it is not possible entirely to establish. Due to this fact, this paper will take into account only those specific names which can be certainly established to be synonyms, i.e. relating to the same populations, but most of names introduced by BOURGUIGNAT (1880), as well as by WESTERLUND (1886), must be omitted and ignored.

For this work I used the abundant collection gathered by myself in the territory of Yugoslavia, North Italy and Greece, as well as S. BRUSINA's collection in the National Zoological Museum in Zagreb, which, thanks to Director Dr. Canedjija, I had the opportunity of examining.

I found out that in the genus *Emmericia* four species can be distinguished, which replace each other geographically, while the fifth (*E. gissensis*), mentioned by BRUSINA (1904) from the island of Pag, I could not find there up to now and I leave it open to question.

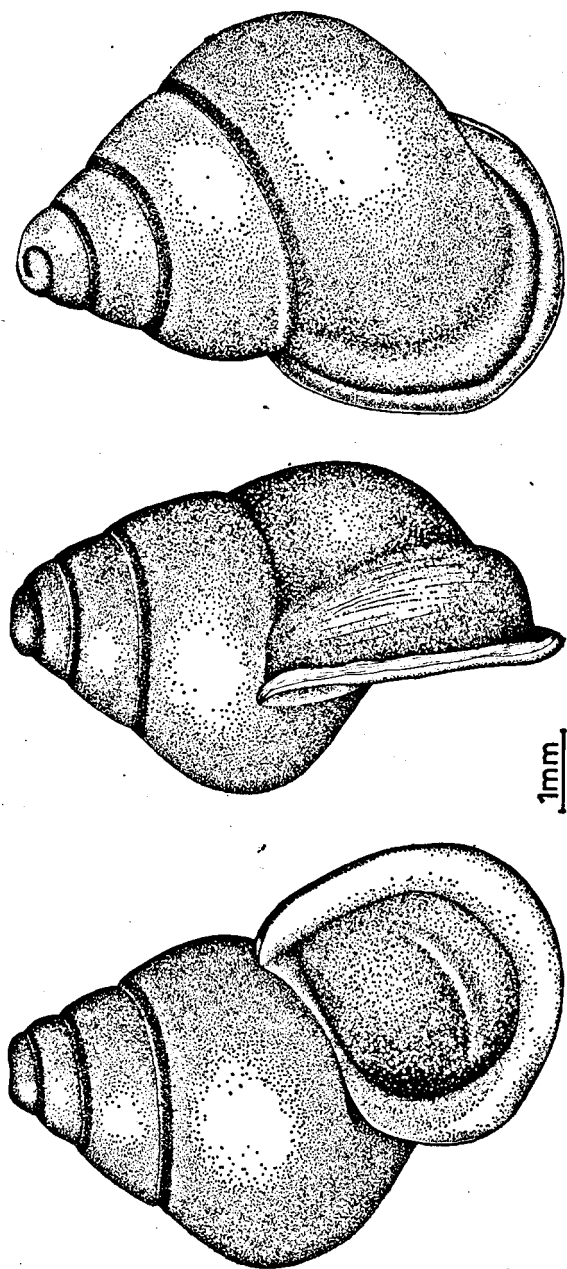


Fig. 1. *Emmericia patula* Brumati.

DIAGNOSIS OF SPECIES

Emmericia patula (Brumati, 1838) (typus generis; fig. 1; syn.: *E. patula* var. *belloti* Brusina, 1870 (= *Paludina belloti* Jan, MS) from Zrmanja; *E. croatica* Brusina, 1904 (nom. nud.), from Rijecina near Rijeka; *E. ecarinata* Brusina, 1904 (nom. nud.), from the lower Neretva basin).

Shell hard, brown, regularly conical, with blunt apex and $4\frac{1}{4}$ - $5\frac{1}{4}$ moderately tumid whorls which regularly and rather rapidly expand in width. The whorls, separated by a rather shallow suture, are smooth, rather shining, with very fine transverse striations. In rare cases there is a faint outer keel in the middle of the last whorl.

Aperture irregularly pear-shaped, angular at the top; the margins of the aperture thickened, reflexed outwards, the outer and the lower lip considerably broader than the columellar one; all the margins on the inner side coated by a shining white pearl lining. The peristome continuous, closely applied to the last whorl. At the top of the aperture, at the transition of the outer into the columellar lip, there is a slight depression.

Near the end of the last whorl, behind the outer lip of the aperture, there is a strongly developed crescentic dilatation, resembling a wide fold or crease, to which on the inner side of the aperture a groove or niche of the same shape corresponds.

Original locality: the source of the Timava, in the vicinity of Trieste. The range of this species: from Monfalcone in Italy up to the Neretva in Yugoslavia. The altitude of these localities varies from 1-70 m. Due to its relatively extensive range, this species varies considerably in the size and form of its shell.

For the other species of this genus only the differences from the generotype are given.

Emmericia narentana Bourguignat, 1880 (a MS name of KLECAK; fig. 2; syn.: *Paludina carinata* Kuzmic, 1858, nom. nud., according to BRUSINA, 1904).

Shell rather straight in outline, the curvature of the whorls being flattened and suture shallow; a strong keel is always present, running somewhat above the suture and passing through the middle of the last whorl. Such a shape (keel and rather flat whorls) gives the shell a pyruloid look. The margins of the aperture more reflexed outwards and the crease behind the outer lip more prominent than in the generotype.

Original locality: the lower course of the river Neretva, in fresh water. This species has a very small range in the extreme lower part of the Neretva valley. No locality exceeds the altitude of eight meters and all, except the original one, in the river itself, are on the left side of the Neretva.

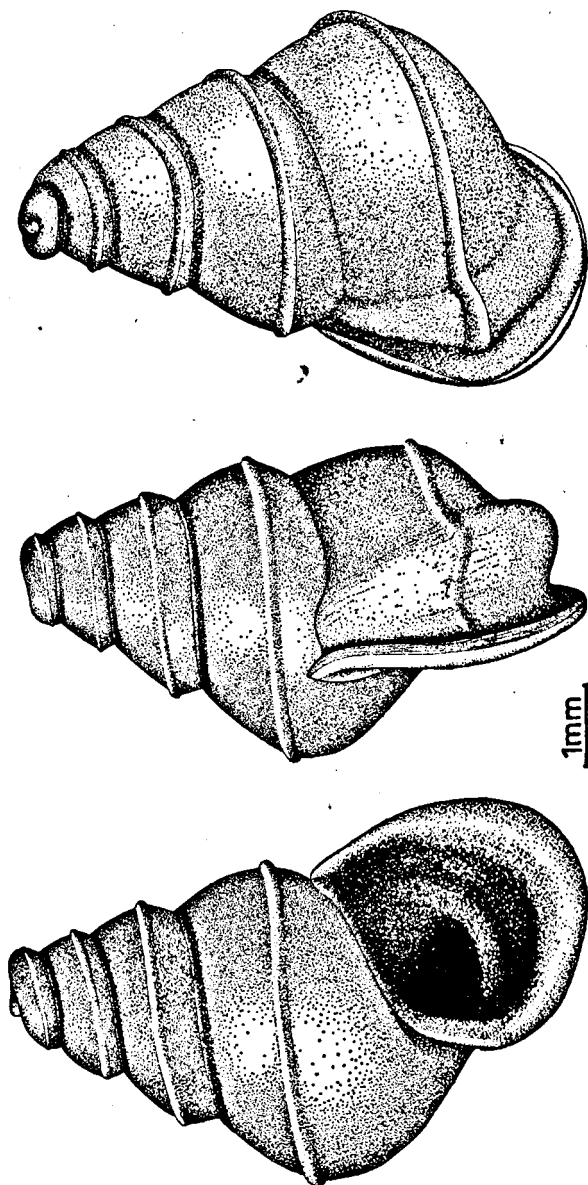


Fig. 2. *Emmericia narentana* Bourguignat.

Emmericia expansilabris Bourguignat, 1880 (a MS name of MÜHLFELD, found as a nom. nud. in several lists since MENKE, 1828; fig. 3; syn.: *Paludina scalaris* Kuzmic, 1858 (nom. nud.), a MS name of NEUMAYER; *E. montenegrina* Bourguignat, 1880; *E. stagnensis* Brusina 1904 (nom. nud.)).

Shell conical, somewhat slender, rather elongate, with more tumid whorls. Very rarely some specimens have a hardly noticeable keel in the middle of the last whorl. The margins of the aperture rather less thickened than in the generotype, never reflexed outwards; there are many specimens with nearly flat margins (when they resemble *Hydrobia*). Ordinarily the crease is absent behind the outer lip of the aperture, although in rare specimens traces of it can be seen.

Original locality: the source of the Rijeka Dubrovacka (Ombla), near Dubrovnik. The altitude of all these localities, except that of Trstena (90 m) is very low.

Emmericia ventricosa Brusina, 1870 (a MS name of KUTSCHIG; fig. 4; syn.: *E. klecaki* Bourguignat, 1880; *E. emotensis* Brusina, 1886, a MS name of KLECAK).

Shell greenish, more shortened, mainly roundish (whereas in other species the ratio of the shell width to its height is about 67 %, in this species this ratio reaches 78, 79 %). Strongly tumid whorls very rapidly expanding in width, so that the fully developed last whorl constitutes the greatest part of the shell. In very rare cases the rudiment of a keel can be detected in the middle of the last whorl. The margins of the aperture thickened but very little reflexed outwards. The crease behind the outer lip of the aperture absent, although in rare cases traces of it can be seen.

Original locality: the brook of Vojskova, in the valley of the upper course of the Cetina. The altitude of most of the localities of this species varies from 239-370 m, and only Buna (71 m), Bregava near Stolac (58 m) and the part of the Neretva in which this species lives, are at a lower altitude. But this species can be found neither in the lower course of the Bregava nor in the river Neretva itself near the mouth of this its tributary. Thus one part of the Neretva, between the localities of *E. ventricosa* and *E. narentana*, is not inhabited by this genus and there is no mixture of the mentioned species in the Neretva river, as was wrongly stated by BRUSINA.

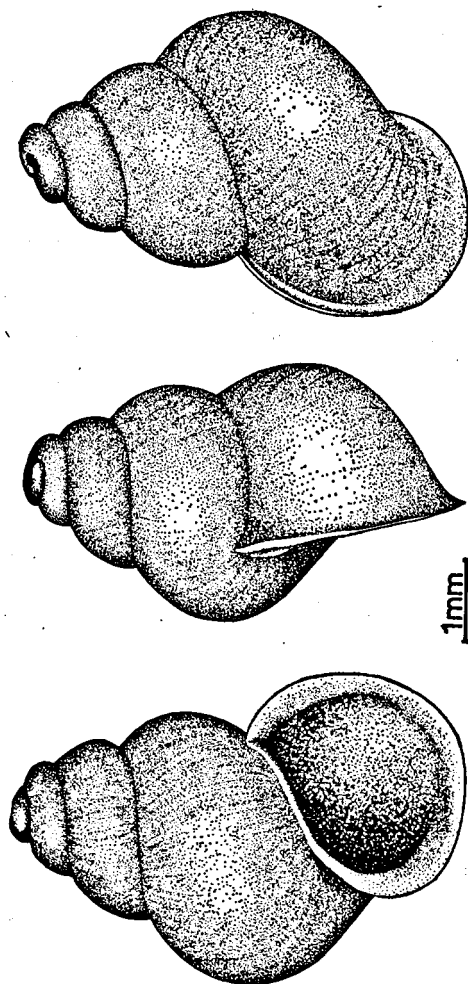


Fig. 3. *Emmericia expansilabris* Bourguignat.

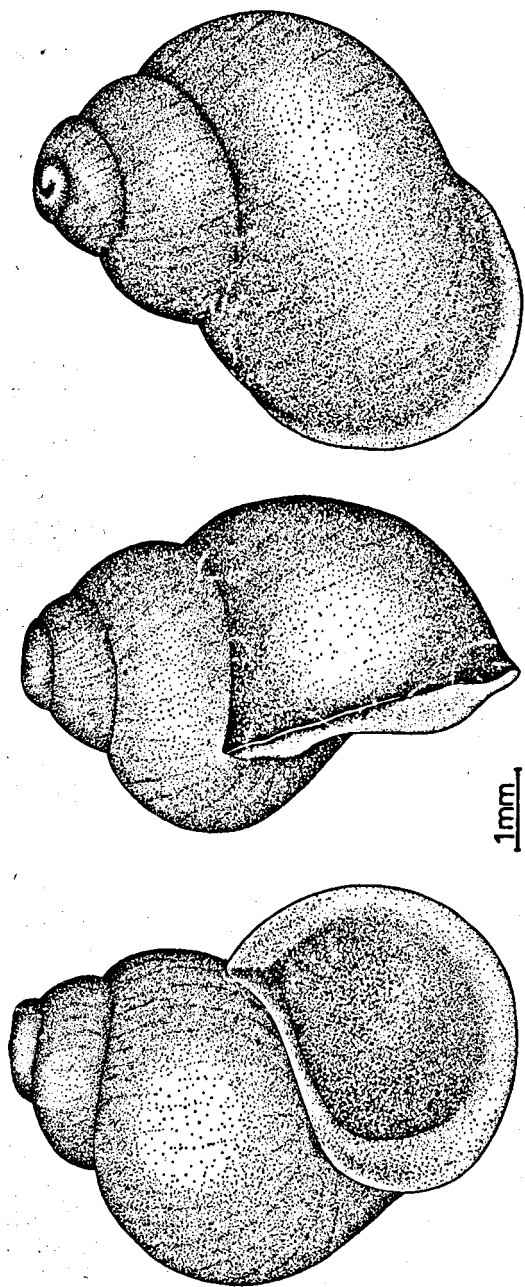


Fig. 4. *Emmericia ventricosa* Brusina.

In table 1 some shell measurements of *Emmericia* species are given.

TABLE 1

Species	Whorl number	Shell measurements (in mm)			
		In the original locality		In all range	
		length	width	length	width
<i>Emmericia patula</i>	4 $\frac{1}{4}$ -5 $\frac{1}{4}$	6.4-8.2	4.5-5.6	5.5-9.5	4.0-6.5
<i>E. narentana</i>	4 $\frac{3}{4}$ -5 $\frac{1}{4}$	6.5-8.7	4.0-5.5	6.0-9.0	4.0-5.5
<i>E. expansilabris</i>	4 $\frac{1}{4}$ -5	5.0-6.5	3.5-4.4	5.0-7.0	3.3-4.9
<i>E. ventricosa</i>	3 $\frac{1}{4}$ -4 $\frac{1}{4}$	5.5-7.0	4.5-5.5	5.0-8.0	4.0-6.0

The anatomical structure of this genus (fig. 5-8) is mainly similar to that of other genera of this family previously anatomically investigated (KRULL, 1935, RADOMAN, 1955, 1965, 1966) but *Emmericia* has its anatomical specificity, which will be given in the description of the genus.

DIAGNOSIS OF THE GENUS *Emmericia* BRUSINA, 1870

Shell regularly conical, rarely roundish, with blunt apex. A keel is characteristic, the strength of which varies from clearly prominent to hardly noticeable in the species where smooth specimens prevail. Aperture pear-shaped, narrowed at the top; the margins of the aperture more or less widened, usually reflexed outwards. Umbilicus slit-like, rarely closed. A crease or fold is characteristic behind the outer lip of the aperture, which is in some species very prominent, whereas in others, but only in rare specimens, it is poorly developed.

The central tooth of the radula (fig. 5) without basal cusps. Lateral tooth usually without clearly differentiated little teeth, which either have grown together or are closely applied to one another.

The female reproductive system (fig. 6) with a clew-shaped loop of the oviduct; only one spermatheca and a large genital atrium are present, both situated entirely inside the tissue of the posterior part of the accessory gland. The male copulatory system (fig. 7) is characterized by a penis with three branches: through the first (from the right) the vas deferens drains, through the central one a duct of a gland which is situated in the penis itself, and through the third (left) the zigzag final part of the long duct of the gland situated in the body cavity.

The nervous system (fig. 8) with shortened pleuro-supraintestinal connective, without a ganglionic thickening on the tentacle and the lateral pedal nerve.

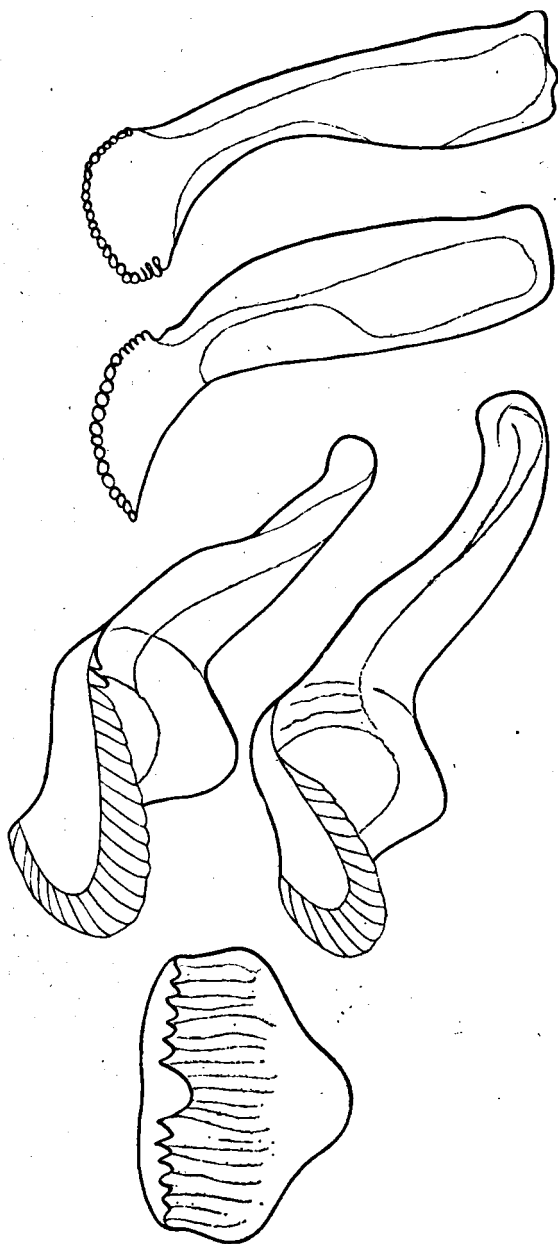


Fig. 5. *Emmericia patula* Brumati; radula.

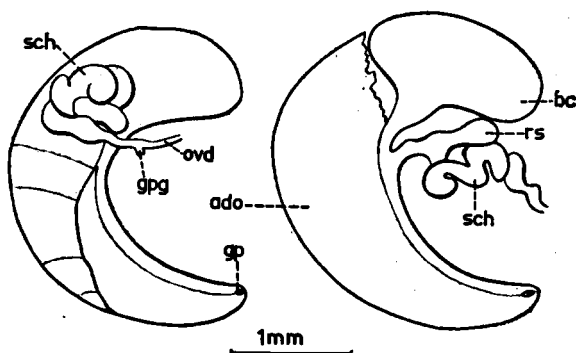


Fig. 6. *Emmericia patula* Brumati; female reproductive system (without ovary), *ado*: accessory gland of oviduct, *bc*: genital chamber (bursa copulatrix), *gp*: genital pore (gonoporus), *gpg*: gono-pericardial duct, *ovd*: ovarian tube (oviduct), *rs*: seminal receptable (receptaculum seminis), *sch*: loop of oviduct.

ZOOGEOGRAPHICAL CONSIDERATIONS AND THE PROBLEM OF SPECIATION

The genus *Emmericia* is now limited exclusively to fresh waters in the Adriatic drainage area, from Italy in the north-west to the gulf of Boka Kotorska in the south-east (fig. 9). In this relatively small area only four species live, which inhabit clear karst waters, springs, streams and rivers. The range of each species makes to a certain extent a geographical and historico-geological unity:

1. The range of *E. patula* is entirely situated north-west of the line Peljesac-Gargano, along the north Adriatic coast (where in the course of geological history regressions and transgressions alternated, with considerable oscillations of the shore lines).

2. *E. narentana* has the smallest range: it lives in several springs in the Svitavsko blato by Neretva and in the extreme lower course of this river, approximately from the mouth of the Krupa up to the beginning of the brackish water.

3. *E. expansilabris* extends from Peljesac up to the gulf of Boka Kotorska, along the south Adriatic coast.

4. *E. ventricosa* lives at the altitude of approximately 300 meters and inhabits the system of "karst poljes" from the Sinj up to the Popovo polje.

As we see, only the last species can be considered "highland" and "continental", whereas the other three inhabit a relatively narrow littoral zone.

It is very difficult to speak about the origin and the ways of differentiation of these species. BRUSINA (1908) thinks that in the

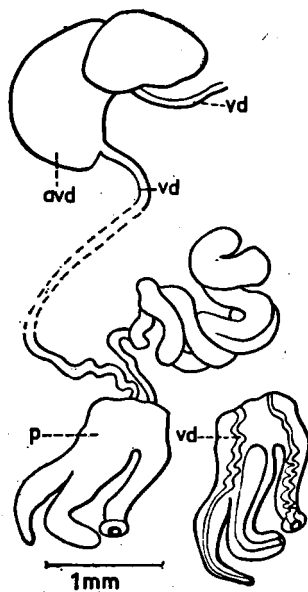


Fig. 7. *Emmericia patula* Brumati; male reproductive system (without seminal gland), the first sketch: natural position, the second sketch: special preparation, *avd*: accessory gland of vas deferens, *p*: penis, *vd*: vas deferens.

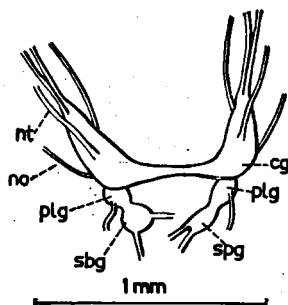


Fig. 8. *Emmericia patula* Brumati; nervous system, *cg*: cerebral ganglion, *no*: nervus opticus; *nt*: nervus tentacularis, *plg*: pleural ganglion, *sbg*: subintestinal ganglion, *spg*: supraintestinal ganglion.

Tertiary *Emmericia* lived "on this side of Velebit, in Serbia and Slavonia" (apparently, he thinks of the Black Sea area of the Dinarides). Later it "retreated about the Adriatic Sea" and there from the fossil *E. canaliculata* Brusina (1870 and 1897)—found by this author in the vicinity of Sinj in Dalmatia, in neogenic fresh-water layers—the Recent species diverged.

Such a statement, which implicitly supposes that in the Neogene *E. canaliculata* had a range not smaller than the present area of the genus, is undoubtedly difficult to explain. Historico-geological data indicate that in the Oligocene the formation of the Alps and the Dinarides was already advanced and that these mountain ranges were mainly formed on the transition from the Paleogene into the Neogene. According to the description and figure I can say that *E. canaliculata* has some similarities with *E. ventricosa*, which now lives in the Sinj polje, a part of the range of this species.

On the Tertiary distribution of the genus *Emmericia* (on both sides of the Dinarides or only on that of the Black Sea), about which BRUSINA speaks, I should, first of all, say the following: some of these fossil findings I had the opportunity of seeing and I must say that one needs much imagination to determine them as representatives of the genus *Emmericia*. Taking into consideration great mistakes made up to now in determining some Recent malacological forms on the basis of the shell only (see something about it in Radoman, 1966) and comparing recent species of *Emmericia* with the above mentioned fossil findings, I am far from believing that here are really involved the fossil representatives of this genus. I am rather inclined to believe that the fossil findings recorded "from Serbia and Slavonia" cannot be considered as reliable evidence for the Tertiary distribution of the genus *Emmericia* spoken of by BRUSINA.

This is why I should try to approach the question of the origin of the recent species of this genus quite differently.

Emmericia would be also primarily (not only secondarily) an Adriatic drainage area form, and its origin would be closely connected with the historico-geological changes of this part of the Balkans. Several important facts support the supposition that the differentiation of these species happened in the Mediterranean area of the Dinarides. Thus, now *E. ventricosa* (nor any species of the genus *Emmericia*) does not reach anywhere the altitude of 400 metres. So it is very interesting that in the Livno polje, situated at an average of 709 m (the lowest point 704 m), there is no species of *Emmericia*. No species of this genus can be found in Lika either, the average altitude of which is 580 m (the lowest point 485 m), although BRUSINA (1908), starting from his supposition about the Tertiary distribution of *Emmericia*, supposed that this genus would be in Lika.

The fact is, however, that *Emmericia* now cannot be found in the

springs and other waters in the upper reaches of the Neretva valley, e.g. in the Radobolja near Mostar, and in numerous springs from Mostar northwards, the altitude of which is considerably below 400 metres. I consider that in the Tertiary these parts of the Neretva valley would have been at a higher altitude. By their subsequent subsidence, some localities of *E. ventricosa* sank to an exceptionally low altitude of 60-90 m (e.g. the Buna and upper Bregava), and the biotopes mentioned which are now without representatives of this genus—due to their post-Tertiary subsidence—came “in the zone” of its recent spread. Naturally, these biotopes could not be subsequently inhabited (by *Emmericia*) due to their territorial isolation. This supposition is consistent with the historico-geological data concerning the glacial and postglacial subsidence of the south-east Adriatic coast, and especially with the subsidence of the lower Neretva area which proceeded over the entire Pleistocene and is still going on.

In support of the Adriatic origin of *Emmericia* we may also mention the fact that this genus cannot now be found anywhere in the Black Sea area of the Dinarides, although there are many biotopes quite similar to those in which *Emmericia* lives in the Adriatic drainage area.

It is conspicuous that the ranges of the Recent species are relatively narrow (each of them is situated within small altitude differences) and elongated, and that, replacing each other geographically, they extend parallel with the recent sea coast (fig. 9). In this respect the range of *E. ventricosa* is characteristic, but the ranges of other species are characteristic as well. Such disposition of these ranges gives the idea that one of the mechanisms of geographical speciation of these species could have been their territorial isolation at the different altitudes and in the different geographical zones (north Adriatic, south Adriatic etc.). Hence it is an interesting phenomenon that in the basin of the same river (for instance of the Cetina or Neretva) two species live, one in the upper, “continental”, and the other in the lower, littoral part.

On the basis of all that has been said, instead of the existing hypothesis, according to which the Recent species of *Emmericia* are the “remains” of a once widespread genus from “both sides of Velebit” (that is from both areas of Dinarides), to us the following seems more probable: the genus *Emmericia* is of Adriatic, namely Mediterranean origin. It is derived from a marine or brackish form which, certainly since the upheaval of the Alps and the Dinarides was already in progress, inhabited the coastal zone of this part of the Tethys. Accordingly, the divergence of the Recent species from an ancestral one started in conditions of a marine, or brackish, environment, in the relatively separated, above mentioned geographical areas. One of the main mechanisms of geographical speciation of this

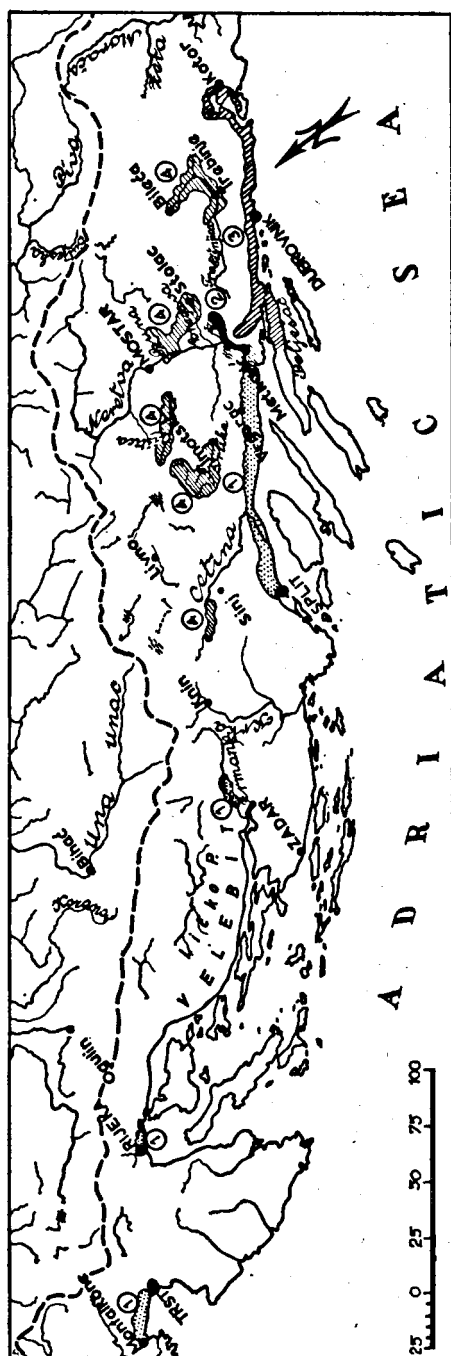


Fig. 9. Map of *Emmericia* distribution in Adriatic area of Dinarides,
1: *E. patula*; 2: *E. narentana*; 3: *E. expansilabris*; 4: *E. ventricosa*.

ancestral form was probably the further upheaval of the Dinarides.

That means, the evolutionary divergence of these species has been connected with the paleogeographic evolution of the Adriatic Sea and the Dinarides as well as of the areas which preceded them. We consider that only in this way is it possible to explain the present distribution of the populations of these species, situated in completely isolated localities, territorially rather distant one from another.

From the above theoretical explanation the question next arises: why did the groups of populations (which we have statistically examined), although completely isolated territorially in several karst poljes and basins, not diverge more one from another and reach at least the subspecies level? This phenomenon can be explained, first of all, by the resemblance of the biotopes in which they lived and still live (stenothermal oligotrophic running karst waters). These resemblances of ecological conditions of life did not stimulate evolutionary divergence, but mainly the parallel evolution of the isolated groups of populations of the same species.

It is not difficult to observe that the group of Recent species of *Emmericia* has all the characteristics of a superspecies: these are very similar and related species, which undoubtedly form a monophyletic group, the ranges of which replace each other geographically (allopatric species). In our opinion, this fact also contradicts the supposition that the Recent species of *Emmericia* (which, as we see, correspond to a superspecies) are the "remains" of a once widespread genus (in which case the "composition" of its species probably would be more heterogeneous).

CONCLUSIONS

1. In this paper the conchylio-anatomical diagnosis of the genus *Emmericia*, of its generotype *E. patula* and three other Recent species, as well as their zoogeographical interrelations, are given.

2. In anatomical characteristics, especially in the structure of the female reproductive system and the nervous system, *Emmericia* is more similar to the genus *Lithoglyphus* than to any other hitherto anatomically investigated hydrobiid genus.

3. *Emmericia* now lives exclusively in fresh waters of the Adriatic drainage area, from Monfalcone in Italy to Boka Kotorska in Yugoslavia. Hitherto fossil records of Tertiary distribution of this genus in the Black Sea area of the Dinarides cannot be considered reliable. On the contrary, several facts favour the supposition that *Emmericia* is primarily, not only secondarily, of Adriatic, i.e. of Mediterranean origin.

The representatives of the genus cannot now be found in any fresh-water locality in the Black Sea drainage area, although there are many biotopes quite similar to those in which *Emmericia* lives in the Adriatic drainage area.

In contrast with several other Hydrobiidae, *Emmericia* does not exceed the altitude of 400 metres.

4. The ranges of *Emmericia* species represent historico-geological unities (north Adriatic coast, south Adriatic coast, lower Neretva valley, system of Dinaric karst-poljes at the average altitude of 300 metres). They are narrow and elongated, and extend parallel with the sea coast. In the basin of the same river (e.g. of the Neretva or Cetina) two species live, one in the upper and the other in the lower part of the valley.

5. To these closely related species, certainly consisting of a monophyletic group of geographically representative (i.e. allopatric) species, whose ranges do not overlap but replace each other geographically, the rank of a superspecies may be assigned. Most probably, these species are the result of geographical speciation. Their origin would have been closely connected with paleogeographical evolution of the Adriatic Sea and the Dinarides, as well as with that of the territories which preceded them. It is possible that one of the main mechanisms of geographical speciation of this genus, which most likely is derived from a marine or brackish ancestor, was the upheaval of the Dinarides.

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